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Pholiota gallica nom. nov., based on *P. lubrica* var. *obscura*

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Abstract — The type of *Pholiota lubrica* var. *obscura*, a forgotten European fungus that has never been critically revised, was morphologically and molecularly examined. It was found to be phylogenetically distant from typical *P. lubrica* and morphologically distinct by its ovoid spores and other characters that place it in *Pholiota* sect. *Spumosae*. It differs from all other European species of sect. *Spumosae* by its unique combination of large fruitbody, castaneous brown pileus, stipe distinctively ornamented by scales or thick bands of bright yellow floccules, and growth on soil in thermophilous Mediterranean forests. For these reasons, we raise its rank to species as *Pholiota gallica* nom. nov., a replacement name required because the epithet *obscura* is already occupied in *Pholiota*. A discussion on similar European and North American species is included. *Pholiota virescentifolia* judged to be synonymous with *P. mixta*.

Key words — *Basidiomycota*, *Agaricales*, taxonomy, nomenclature, phylogeny

Introduction

Although several critical studies of the genus *Pholiota* in Europe have been published in last three decades (Jacobsson 1991, Holec 2001, Noordeloos 2011), there are still problems waiting for revision. One concerns *Pholiota lubrica* var. *obscura,* a fungus diagnosed by its robust stature, castaneous brown pileus, and stipe ornamented with big yellow floccules (Bon & Chevassut 1989). Holec (2001: 197) has been the only recent author to treat the variety. Its ovoid spores exclude this fungus from *P. lubrica* (diagnosed by phaseoliform spores in side view) and place it among species of *Pholiota* sect. *Spumosae*, characterised by ovoid spores. A detailed type study and comparison with similar taxa were necessary to evaluate taxonomic position of *Pholiota lubrica* var. *obscura*. The aim of this paper is to resolve the question using both morphological and molecular methods.

Table 1. Collections* used for DNA analysis.
(Collections sequenced for this paper are in bold.)

Collection	Country	Publication	DNA sequence	Voucher
P. castanea	USA	Matheny & Wolfenbarger, unpubl.	HQ222025	TENN020269
P. decussata	Italy	Osmundson et al. (2013)	JF908583	MCVE 11237 (paratype of *P. chocenensis*)
P. ferrugineo-lutescens	USA	Matheny & Wolfenbarger, unpubl.	HQ222026	TENN028897
P. gallica	**France**	**This paper**	**HG007988**	**MPU: Herbier Chevassut 3478** (holotype)
P. highlandensis	**Czech Rep.**	**This paper**	**HG007976**	**PRM 888152** (as *P. carbonaria*)
P. highlandensis	**Czech Rep.**	**This paper**	**HG007974**	**PRM 887239** (as *P. carbonaria*)
P. lenta	Italy	Osmundson et al. (2013)	JF908582	MCVE 7100
P. lenta	Finland	Guzmán-Dávalos et al. (2003)	AY281022	H, IBUG: R. Tuomikoski s.n.
P. lubrica	**Czech Rep.**	**This paper**	**HG007987**	**PRM 915546**
P. lubrica	**Czech Rep.**	**This paper**	**HG007986**	**PRM 899117**
P. lubrica	Japan?	Maeta et al. (2008)	AB301612	NBRC32453
P. mixta	**Czech Rep.**	**This paper**	**HG007979**	**PRM 909924**
P. spumosa	Italy	Osmundson et al. (2013)	JF908577	MCVE 3533
P. spumosa	**Czech Rep.**	**This paper**	**HG007983**	**PRM 897683**
P. spumosa	**Czech Rep.**	**This paper**	**HG007981**	**PRM 897147**
P. squarrosa	USA	Matheny et al. (2006)	DQ494683	PBM 2735 (also in CUW)
P. virescentifolia	USA	Matheny & Wolfenbarger, unpubl.	HQ222029	TENN020591

*Almost all available GenBank sequences from *Pholiota* sections *Spumosae* and *Lubricae* were included. Those omitted were: *P. mixta* EU715686 (Mexico; risk of misidentification); *P. flavida* JF908576 (Italy; identity unclear, as the name has been used in different senses); *P. lubrica* JF 908578 (Italy; = *P. lenta*, according to DNA data); and *P. spumosa* AY781268, AY618246, and *P. carbonaria* JF440578, GU934596, AY251301 (environmental samples not based on critically identified vouchers).

Materials & methods

Morphology

The holotype of *P. lubrica* var. *obscura* was loaned to the first author directly from G. Chevassut in 2002. After Chevassut's unfortunate death in 2003, the holotype was retained in PRM herbarium (Mycological Department, National Museum, Prague, Czech Republic) as it was unclear whom to return it. In 2013 it was sent to MPU herbarium (Institut de Botanique, Université Montpellier 2, France), the current 'home' of Chevassut's herbarium. (For herbarium acronyms, see Thiers 2013.) The type was studied by traditional taxonomic methods as set forth in Singer (1986), Bas et al. (1988), and Holec (2009). Microscopic mounts were made in a 5% KOH solution and studied

under an Olympus BH-2 light microscope. Spore sizes are presented as the main data range (c. 10–90 percentile values) flanked by extreme values (in parentheses) of all spores measured (20 measurements per collection). The spores were measured directly in the microscope using the eyepiece micrometer. Q = the length/width quotient of all spores and Qav = mean value of Q.

Phylogeny

DNA was isolated from dried specimens as described in Holec & Kolařík (2013). The ITS-LSU rDNA gene was amplified using primers ITS1F and LR6; the same primers, together with primers ITS4 and NL1, were used for sequencing. Sequences were combined with published *Pholiota* ITS-LSU rDNA sequences (Tab. 1) selected from GenBank based on the greatest similarity using BLAST search and subsequent phylogenetic analysis (trees not shown). The dataset was aligned in MAFFT v6.861b (Katoh & Toh 2008). *Pholiota squarrosa* (Vahl) P. Kumm., a taxon sister to our sequences in the preliminary tree, was selected as outgroup. Of the total 17 sequences (eight obtained in this study) and 693 positions in the final dataset, 132 were variable and 91 parsimony informative. The evolutionary history was inferred by the Maximum Parsimony method in MEGA 5.0 (Tamura et al. 2011) using default settings and 300 bootstrap replicates. Bayesian phylogenetic analyses were conducted as described in Holec & Kolařík (2013) using a K2H-I substitution model.

Taxonomy

Morphology

Our holotype study (see below) confirmed the original observation by Bon & Chevassut (1989) that *P. lubrica* var. *obscura* has ellipsoid-ovoid to ovoid spores. For this reason it cannot belong to *P. lubrica* (Pers.) Singer, which is characterized by phaseoliform spores in side view (Holec 2001). *Pholiota lubrica* is the type species of *Pholiota* sect. *Lubricae* (Fr.) Singer (emend. Holec 2001) that is delimited by phaseoliform spores and comprises three European species: *P. lubrica*, *P. lenta* (Pers.) Singer, and *P. elegans* Jacobsson. [Jacobsson (1991) and Noordeloos (2011) used the name *P.* sect. *Lubricula* Kühner, a synonym of *P.* sect. *Lubricae*.]

Its ovoid spores place *P. lubrica* var. *obscura* in *Pholiota* sect. *Spumosae* A.H. Sm. & Hesler (emend. Jacobsson 1991), represented in Europe by *P. spumosa* (Fr.) Singer, *P. mixta, P. highlandensis* (Peck) Quadr. & Lunghini, *P. brunnescens* A.H. Sm. & Hesler, and *P. chocenensis* Holec & Kolařík (Holec 2001, Holec et al. 2014, Noordeloos 2011). These species are very similar microscopically and are delimited based on mostly macromorphological and ecological characters.

Pholiota lubrica var. *obscura* differs from all species of sect. *Spumosae* by its unique combination of characters: large fruitbodies, castaneous brown pileus, stipe distinctively ornamented by scales or thick bands of bright yellow floccules, and growth on soil (not on burnt wood, charcoal, or ash) in thermophilous Mediterranean forests.

Phylogeny

Our sequence analyses of representatives of sects. *Spumosae* and *Lubricae* support the conclusions of our morphological analyses. The phylogenetic tree (Plate 1) placed with high statistical support the sequences of *P. lubrica* var. *obscura* and the typical *P. lubrica* on very distant clades. The *P. lubrica* var. *obscura* sequence comprises 698 readable positions and a string of 57 positions in ITS2 that are superimposed, even in repeated sequencing of independently amplified PCR amplicons. This sequence, when aligned with *P. lubrica* (536 positions), differs in 11% of the positions.

Pholiota lubrica var. *obscura* forms a strongly supported lineage with *P. highlandensis* (sect. *Spumosae*) and two GenBank entries (*P. castanea, P. decussata*). However, both the American *P. castanea* and an Italian collection identified as *P. decussata* (Osmundson et al. 2013) form a separate clade. The sequence of *P. decussata* sensu Osmundson et al., which represents *P. chocenensis*

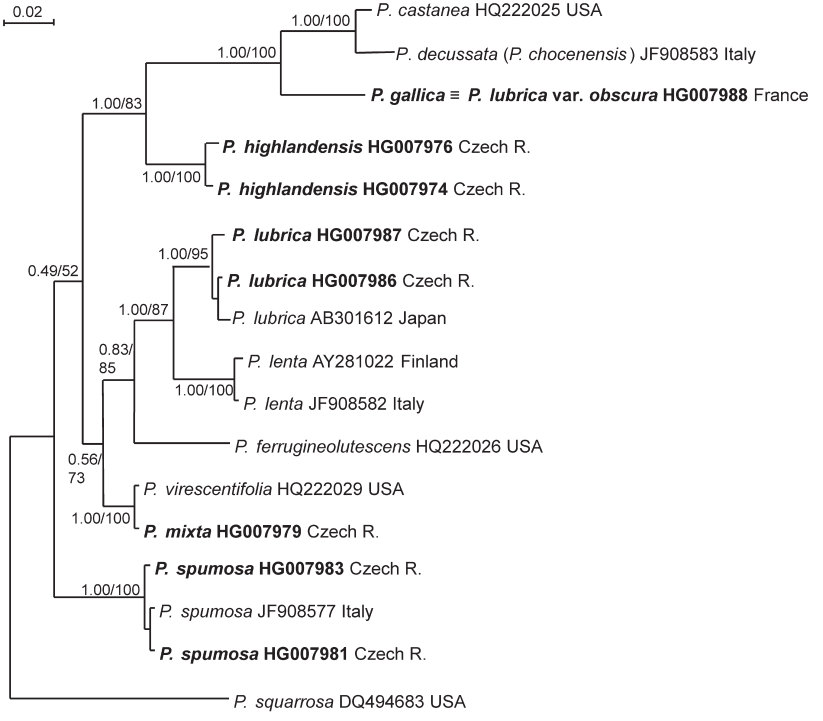

Plate 1. Phylogenetic placement of *Pholiota gallica* inferred from ITS rDNA data. MrBayes tree topology is presented; numbers beside the nodes represent Bayesian MCMC posterior probabilities and parsimony bootstraps. Sequences printed in bold were obtained during this study.

(Holec et al. 2014), differs from that of *P. lubrica* var. *obscura* by 18%. The species traditionally classified in sect. *Lubricae* — *P. lubrica*, *P. lenta*, and the American *P. ferrugineolutescens* — form a second well-supported lineage. Other members of sect. *Spumosae*, *P. mixta* (European)/*P. virescentifolia* (American) and *P. spumosa*, form two independent phylogenetic lineages. The mutual positions of these four main species groups are unresolved. Our data suggest that species of the traditionally recognized sect. *Spumosae* form several well-supported lineages related to the species lineage from sect. *Lubricae*. Thus, sect. *Spumosae* appears paraphyletic and contains some *Lubricae* species. Broader taxon sampling and additional molecular markers are needed to determine if both sections represent natural monophyletic groups or if the higher ranked taxon – *Pholiota* subgen. *Flammuloides* A.H. Sm. & Hesler (= *P.* subgen. *Lubricula* Kühner) – is the monophyletic group containing all the species mentioned.

Taxonomic position of *P. lubrica* var. *obscura*

The most important conclusions from our morphological and DNA analyses are that (1) *P. lubrica* var. *obscura* is clearly distant from the typical *P. lubrica*, (2). *P. lubrica* var. *obscura* is also distant from other European representatives of *Pholiota* sects. *Spumosae* and *Lubricae* as well as from its nearest relatives in the *P. highlandensis* clade, and (3) *P. lubrica* var. *obscura* is separated by a unique combination of morphological and ecological characters. For these reasons, it is raised to species rank below.

Pholiota gallica Holec & Kolařík, **nom. nov.** Plate 2

MycoBank: MB804715

Etymology: from *Gallia*, the Latin name for today's France, the type locality.

≡ *Pholiota lubrica* var. *obscura* Bon & Chevassut, Doc. Mycol. 19(75): 44. 1989. [non *Pholiota obscura* A.H. Sm. & Hesler, N. Amer. Species *Pholiota*: 108. 1968].

Type: France, Languedoc, Maison forestière des Plots, 350 m a.s.l., under *Pinus halepensis*, 24.XI.1985, leg. Durand, herb. G. Chevassut no. 3478 (holotype, MPU!; GenBank HG007988, as P. *lubrica* var. *obscura*); 10 km N of Montpellier, Bellevue, under *Quercus ilex*, 24.XI.1968, herb. G. Chevassut no. 600 (paratype, MPU; not seen; loan request not acknowledged).

Original diagnosis (Bon & Chevassut 1989): *A typo differt pilei coloribus obscurioribus (brunneis ad instar* Suilli lutei*), stipite conspicue luteo-armillato, lamellis sporisque fuscioribus quam in typo. Micro sicut in typo sed sporae interdum usque ad 8(8.5) × 5–5.5 µm, pariete s.l. +/- brunneola.*

Original line drawings: Doc. Mycol. 19(75): p. 43, fig. 25, 1989.

English translation of the original French description — A large *Pholiota*, with castaneous brown pileus and stipe ornamented with big yellow floccules. Pileus 4–9 cm, cuticle viscid, bright brown (like *Suillus luteus*); lamellae rather broad (≤1 cm), rather dense, emarginate, pale olivaceous yellow or somewhat darker; stipe 3–7 × 1–1.2 cm, subcylindrical, distinctively

ornamented (starting several cm under the lamellae) by bright yellow floccules which are very characteristic (scales or thick bands); CONTEXT thick, white, odour weak, of leather. SPORES 5.5–7.5(–8.5) × (4.5–)5–5.5 µm, ovoid with an indistinct germ pore and wall rather dark for a *Pholiota* s.str.; CYSTIDIA variable, clavate, ventricose or lageniform, 40–60 × 12–15 µm, ± yellow on apex in ammonia but only slightly cyanophilous in C4B; CHEILOCYSTIDIA of the same type but ± intermixed with marginal cells of variable shape, clavate, fusiform or lageniform and ± constricted, hyaline; EPICUTIS a remarkably gelatinized ixotrichoderm, hyphae 2–5 µm; PIGMENT of several types (mixed) or membranally encrusting towards the subcutis; CLAMPS numerous.

Holotype study

The holotype consists of two well-dried mature fruitbodies. BASIDIOSPORES 6.8–8 × 4.4–4.8(–5.2) µm, Q = 1.38–1.73, Qav = 1.55, ellipsoid-ovoid to ovoid in face view, ovoid in side view, rusty yellow, wall thick, rusty brown, with a narrow but distinct germ pore, hilar appendix indistinct; BASIDIA 24–27 × 6–7 µm, 4-spored, narrowly clavate with median constriction; BASIDIOLAE 16–20 × 6–7 µm, clavate; LAMELLAE EDGE fertile; CHEILOCYSTIDIA numerous, protruding, 42–56 × 10–12 µm, fusiform to lageniform with narrow pedicel (1.5–3 µm), thin-walled, sometimes with apical yellow incrustations, mostly hyaline or some partly filled with a homogeneous pale yellow content or completely filled with a fine granular rusty yellow substance; PLEUROCYSTIDIA abundant, 56–60 × 12–16 µm, similar to cheilocystidia; CHRYSOCYSTIDIA absent; LAMELLAR TRAMA regular, of parallel hyphae 2–10 µm broad; PILEUS CUTICLE formed by a thin rusty brown epicutis and a thicker rusty yellow subcutis, gradually passing into the pileus trama, non-gelatinized; EPICUTIS of cylindrical hyphae 3–10 µm broad, with strong membranal and encrusting pigmentation; SUBCUTIS of hyphae 10–24 µm broad, formed by cylindrical to slightly fusiformly inflated, thick-walled cells with membranal and encrusting pigmentation, when observed on sections which are not parallel with subcutis hyphae, the subcutis looks subcylindrical, of ellipsoid to subglobose cells, however, these "cells" represent oblique sections through cylindrical hyphae; PILEOCYSTIDIA or distinctively shaped terminal elements absent; STIPE CUTICLE a cutis of densely arranged cylindrical hyphae, (2–)4–10 µm broad, with yellow membranal pigment and yellow-rusty encrustations, covered with cords of more distinctively pigmented hyphae forming the stipe covering, at places forming interwoven and protruding clumps (visible as scales by naked eye) of hyphae 4–12 µm broad; CAULOCYSTIDIA or distinctively formed terminal elements absent; CLAMP CONNECTIONS present in all tissues.

Taxonomic notes

Our morphological observations were very similar to those by Bon & Chevassut (1989). The discrepancies concern the cystidial shape (we did

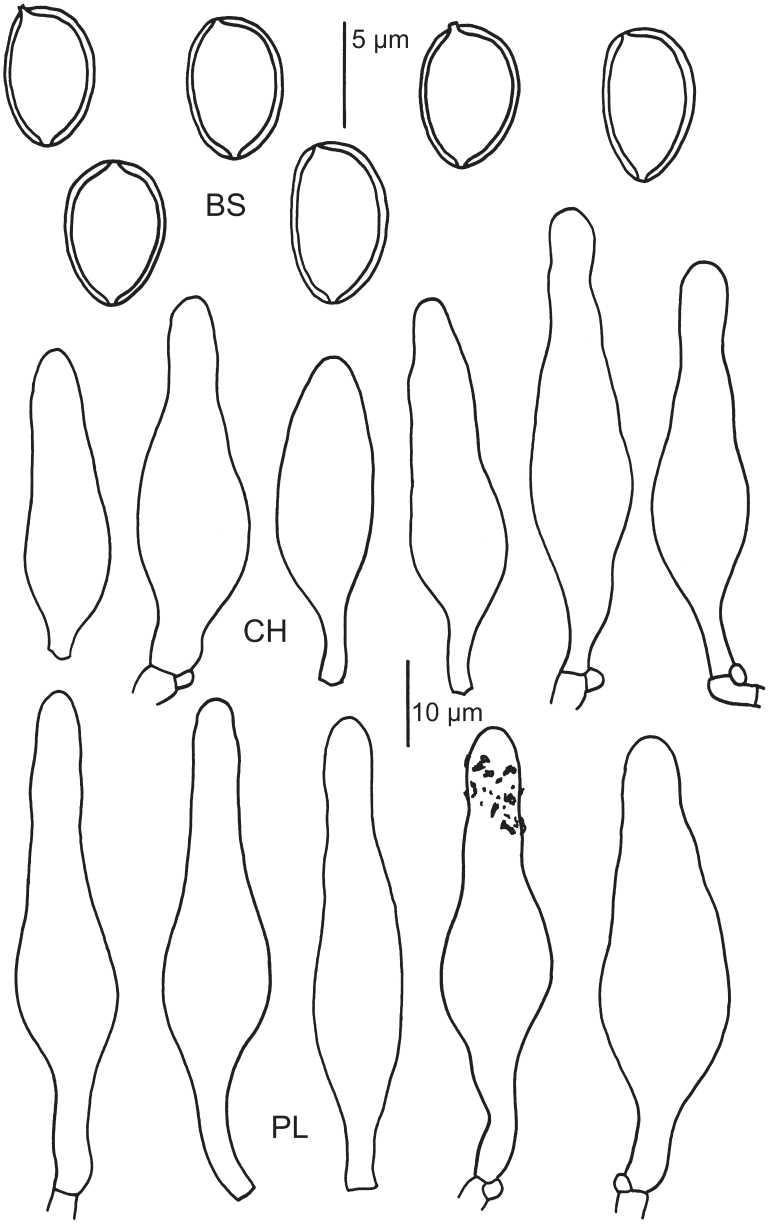

Plate 2. *Pholiota gallica* (holotype, MPU: herb. G. Chevassut no. 3478).
BS: basidiospores, CH: cheilocystidia, PL: pleurocystidia. Drawing by J. Holec.

not observe clavate cystidia) and the character of the pileus cuticle, which was certainly in more natural condition when studied by Bon & Chevassut, who observed an ixotrichoderm that probably collapsed when dried and so resembled the cutis seen by us. The most important *P. gallica* characters are the ovoid spores with a narrow germ pore, numerous fusiform to lageniform cheilo- and pleurocystidia (sometimes with a yellow apex or yellow intracellular pigmentation), and the absence of pileo-/caulocystidia or distinct terminal elements. These characters place *P. gallica* in *Pholiota* sect. *Spumosae*.

Although only two *P. gallica* collections are currently available, the uniqueness and correlation of the morphological, ecological, and DNA characters support the elevation of the original variety to species rank. The taxonomic resolution, awaited for 12 years by the first author (see Holec 2001: 197), was finally powered by our phylogenetic results. We would like to direct the attention of Mediterranean mycologists to *P. gallica* so as to stimulate their search for it. We believe that we offer a better solution than ignoring the forgotten *P. lubrica* var. *obscura,* which, moreover, does not represent the typical *P. lubrica*.

Comment on nomenclature: We intended to raise *P. lubrica* var. *obscura* to the rank of species using the name 'obscura.' However, the previous existence of *P. obscura* A.H. Sm. & Hesler required that we create a replacement name (*P. gallica*) for the species, which shares the holotype of *P. lubrica* var. *obscura*.

Notes on similar European species

We summarize the morphological differences between *P. gallica* and the European species of *Pholiota* sects. *Spumosae* and *Lubricae* in Tab. 2. The species most similar in habit are *P. chocenensis*, *P. brunnescens,* and *P. lubrica*. However, *P. chocenensis* is smaller and has a brighter pileus colour and darker stipe covering, *P. brunnescens* grows on coal and has caulocystidia on the stipe surface (Holec et al. 2014 show that it is probably conspecific with *P. highlandensis*), and *P. lubrica* has slightly phaseoliform spores. *Pholiota gallica* seems to be a Mediterranean species growing under typical thermophilous trees (*Pinus halepensis*, *Quercus ilex*), but further collections are needed to evaluate its habitat preferences more precisely.

Notes on American species

In their North American *Pholiota* monograph, Smith & Hesler (1968) treated many species in *Pholiota* sects. *Flammuloides*, *Carbonicola*, *Spumosae*, and *Lubricae* based on microcharacters that are simultaneously very similar and very variable. Molecular studies would be helpful, but *Pholiota gallica* does not match any of the small percentage of taxa already sequenced (Plate 1).

The morphologically most similar species belong to stirpes *Condensa* and *Spumosa* (Smith & Hesler 1968), neither of which fits *P. gallica*. Within sect. *Lubricae* sensu Smith & Hesler (differently circumscribed than our section *Lubricae*), the most similar taxa are in stirpes *Fibrillosipes* and *Lubrica*. The

Table 2. Pairwise comparisons of characters differentiating *P. gallica* from other European species of *Pholiota* sect. *Spumosae* and *Lubricae**

Taxon	Taxon characters	*P. gallica* characters
P.* sect. *Spumosae	**Spores ovoid**	
P. chocenensis	Rather small (pileus 1.5–5 cm), pileus bright (orange, with yellow-ochre or rusty brown tinge), stipe veil remnants dark (yellow-rusty to rusty orange)	Large (pileus 4–9 cm), pileus dark (castaneous brown), stipe veil remnants yellow
P. highlandensis	Anthracophilous; stipe covering fine, flocculose to fibrillose	Terricolous; stipe covering distinct, forming scales to bands
P. mixta	Rather small (pileus 2–6 cm), pileus margin and stipe whitish, stipe covering fine, fibrillose	Large (pileus 4–9 cm), pileus dark (castaneous brown); stipe covering distinct, forming scales to bands
P. spumosa	Medium-sized (pileus 3–7 cm), yellow-ochre to yellow–brown; stipe covering fine, fibrillose-tomentose	Large (pileus 4–9 cm), pileus dark (castaneous brown); stipe covering distinct, forming scales to bands
P. brunnescens	Anthracophilous; caulocystidia clavate	Terricolous; caulocystidia absent
P.* sect. *Lubricae	**Spores phaseoliform in side view**	
P. lubrica	Pileus orange, cinnamon to reddish-brown with paler margin; spores phaseoliform in side view	Pileus castaneous brown; spores ovoid
P. lenta	Pileus whitish to greyish-beige; spores phaseoliform in side view	Pileus dark (castaneous brown); spores ovoid
P. elegans	Pileus lemon-yellow, yellow to yellow-ochre; spores phaseoliform in side view	Pileus dark (castaneous brown); spores ovoid

*Based on data in this paper, Holec (2001), Noordeloos (2011), and (for *P. chocenensis*) Holec et al. (2014).

species there differ from *P. gallica* in macrocharacters and smaller, more or less phaseoliform basidiospores. However, a final conclusion must await the revision and sequencing of all North American species.

Identity of *P. virescentifolia*

Pholiota mixta (Fr.) Kuyper & Tjall.-Beuk., Persoonia 13: 81. 1986.

≡ *Agaricus mixtus* Fr., Epicr. Syst. Mycol.: 185. 1838.

= *Pholiota virescentifolia* A.H. Sm. & Hesler, N. Amer. Species Pholiota: 363. 1968.

The sequence obtained from the holotype of *P. virescentifolia* forms a strongly supported lineage with the European *P. mixta* (Plate 1). Their morphological characters agree as well, except for tufts of caulocystidia that Holec (2001) did not observe in *P. mixta*. However, the key diagnostic characters are the same in both species: dirty yellow-brown viscid pileus, short stipe with whitish apex, ovoid spores measuring about 5.5–8 × 3.5–4 µm, numerous and large cheilo- and pleurocystidia, and growth on soil and humus (not on wood). We therefore place *P. virescentifolia* into synonymy under *P. mixta*.

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